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TAXONOMY OF THE DEEP SEA FISHES OF THE GENUS *CHAULIODUS*

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No. 9 — Taxonomy of the Deep Sea Fishes of the Genus Chauliodus

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Representatives of the genus *Chauliodus* are found in all the oceans of the world in temperate and tropical regions, and form a rather closely knit group. Some species are widespread in their distribution; others appear to be confined to particular water masses. Among the more widely ranging forms, populations appear to differ from one water mass to another, with the result that a number of species and subspecies have been described.

The various forms of *Chauliodus* are not particularly well defined in much of the literature, nor are they always easy to distinguish when specimens are at hand. The older descriptions, in particular, made no allowance for normal variation within species, and are, almost without exception, so brief and generalized that it is well nigh impossible to determine what form was being described. Yet the authors of the past cannot really be blamed for this. Specimens were even more difficult to obtain in those days than they are now, and taxonomic thought of the time was a far cry from modern ideas.

In 1906, Brauer gave a summary, based on the literature, of the species then known, but it was not until the expeditions of the Dana that a series of specimens adequate for modern taxonomic techniques became available. Basing their account on the specimens collected in the Atlantic by the Dana expedition of 1920-22, Regan and Trewavas (1929) produced the first modern work on *Chauliodus*. They described a new species, *C. danae*, distinguishing it from *C. sloani* chiefly on the basis of the more posterior position of the dorsal fin and a different structure of the chin barbel.

Later, Ege (1948) studied the large collections of *Chauliodus* from the round-the-world Dana cruise of 1928-30. He described two new subspecies of *C. sloani* (*C. s. secundus* from the Indo-Pacific and *C. s. schmidti* from the eastern Atlantic) and reduced several other species to the status of subspecies of *C. sloani*. Haffner (1952b), studying the zoogeography of the genus, accepted Ege's classification, though with some reservations as to the propriety of the subspecific designations of some groups. Since that time, virtually nothing has been done with the group as far

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as published information is concerned, although exploratory fishing, particularly in the north and central Pacific, has added a great deal to our knowledge of the range of several species.

ACKNOWLEDGEMENTS

In carrying out the present work, we have had available to us the large collections from the Dana Expedition 1928-30: the Museum of Comparative Zoology, Harvard University; the United States National Museum; the Department of Oceanography, University of Washington;[1] and the Bingham Oceanographic Collection, Yale University. In addition, we have been able to examine other specimens from the British Museum (Natural History); the Galathea Expeditions 1950-1952; the Marine Laboratory, University of Miami; the Scripps Institution of Oceanography; the Zoological Museum, Stanford University; the Department of Fisheries, University of Washington; and the U.S. Fish and Wildlife Service Laboratory, Honolulu. This material has been made available through the kind cooperation of the following, to whom gratitude and thanks are tendered: Dr. William Aron, Dr. E. Bertelsen, Dr. Henry B. Bigelow, Dr. Anton Bruun, Mrs. M. Dick, Dr. Alfred Ebeling, Dr. Robert Kanazawa, Dr. Ernest Lachner, Dr. Jørgen Nielsen, Dr. C. R. Robins, Mr. R. Rosenblatt, Dr. W. F. Royce, Dr. F. G. W. Smith, Dr. Leonard P. Schultz, Miss M. Storey, Dr. Ralph Taylor, and Dr. Ethelwyn Trewavas.

DIAGNOSTIC CRITERIA

Early descriptions of species of *Chauliodus* depended in the main upon the customary fin ray counts and body proportions.

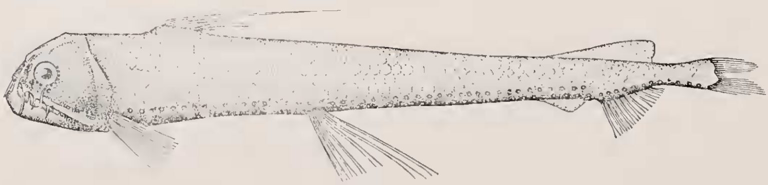

Figure 1. *Chauliodus sloani.* Drawn from several specimens in the Bingham Oceanographic Collection by Shirley P. Hartman.

[1] The material from the University of Washington, Department of Oceanography was collected by Dr. Wm. Aron. His work was supported by the National Science Foundation and by the Office of Naval Research, Contract 477 (10).

Garman (1899) appears to have been the first to realize that the number of serial photophores could be of some taxonomic importance in the group, in which he was followed by Brauer (1906). Ege (1934), studying the related genus *Stomias*, discovered there that the number and arrangement of the small body photophores were characteristic for the various species. In his subsequent work on *Chauliodus* (Ege, 1948), he continued with this same line of thought, placing rather heavy emphasis on the number and type of organ in each scale area, as well as utilizing other characters such as the relative size of certain small body photophores, number and size of teeth, number of lower jaw denticles, etc. However, Ege appears to have based his conclusions with respect to these more minute characteristics upon the examination of a rather small number of specimens. Thus, in dealing with the number and size of the small light organs in the various scale areas, he describes only one or two specimens for each form. Similarly, with respect to teeth and lower jaw denticles, he tabulates data for only four or five specimens of each species. It seemed necessary, therefore, to subject these and other matters to a statistical examination, based on as many specimens as possible.

We therefore turn now to an examination of the various criteria which have been used for the diagnosis of the several species of *Chauliodus*. For this examination, we have used as many specimens as possible of each species. With respect to the serial photophores, we have made use, wherever possible, of the data of other authors as well as our own. It will be noted that there are discrepancies here and there between the number of specimens listed as study material and the number actually used in certain computations. This is due to the delicate nature of these fishes, with the result that they are easily damaged in capture and preservation, so that the character in question could not be observed with the desired degree of accuracy.

Pre-anal distance less head length is measured from the tip of the snout to the base of the first ray of the anal fin. The head is measured from the tip of the snout to the posterior edge of the opercular membrane, with the head as nearly as possible in a normal position. Expressed as a percentage of the standard length, this measurement has been used to set off *C. barbatus* from all other species. However, as shown in Figure 2, *barbatus* is completely overlapped in this respect by *macouni*, and to a great extent by *sloani* as well. To a lesser degree, *schmidti* and *pammelas* also fall within range of *barbatus* for

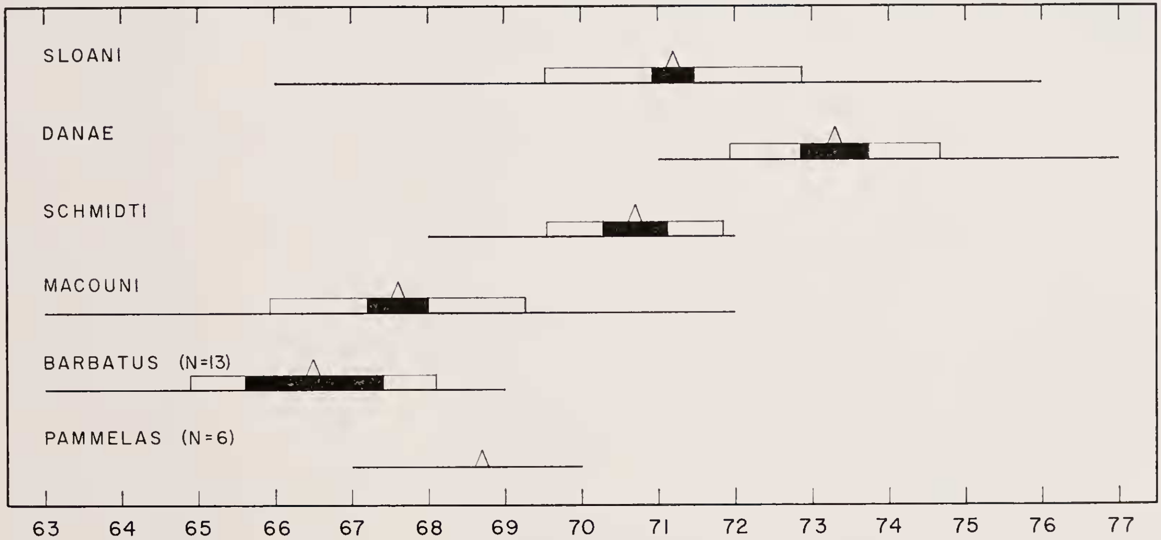

Figure 2. Distribution of pre-anal distance less head length, expressed as percentage of standard length. The range of variation is shown by the heavy base line, with the mean indicated by the point of the inverted V above. One standard deviation and two standard errors on each side of the mean are shown by the white and black bars respectively.

this character. Although some of the differences which appear in Figure 2 are certainly significant, both statistically and biologically, this character is really useful only to separate *barbatus* and *pammelas* from *danae*.

Relative length of third and fourth premaxillary teeth has also been used to separate *barbatus* from the other species. In *C. barbatus,* and also in *C. macouni,* the third premaxillary tooth is always longer than the fourth. In all the other species, the opposite is true. Rarely in *C. sloani* and *C. schmidti* does one find an individual whose premaxillary teeth do not fall into the usual pattern, and the difference in the length of the teeth is usually very slight in such instances. In nearly all the species, there are also occasional individuals whose third and fourth premaxillary teeth are of about equal length, but again, these are rather rare (see Table I). The relative length of the third and fourth premaxillary teeth, then, appears to be a fairly good character for separating the two strictly Pacific Ocean forms from the others.

TABLE I

Relative lengths of the third and fourth premaxillary teeth in *Chauliodus*. The body of the table lists the number of specimens of each species in each category.

Species	3rd tooth longer	4th tooth longer	About equal
sloani	7	101	9
danae	0	36	2
schmidti	2	20	5
pammelas	0	5	0
barbatus	16	0	2
macouni	64	0	2

The number of light organs in each scale area of the second, third and fourth rows has also been considered as diagnostic. In the second row, each scale area generally has two organs in *C. sloani, C. pammelas, C. danae,* and *C. macouni.* In *C. schmidti* and some populations of *C. sloani,* there is a tendency for only a single organ to be present, and in *C. barbatus* it is a rare individual that has more than one much reduced organ present in the second row areas. However, there is a great deal of variation, particularly in *C. sloani,* where we have found 1, 2 or 3 organs in these second row areas. Some indication of this degree of variation is shown in Table II, comparing *C. sloani, C. schmidti* and the *dannevigi* population of *C. sloani.* It is apparent from this table that the number of small photophores in the second row is not diagnostic for *C. schmidti,* although there is a tendency towards reduction in this form. The same is true for the *dannevigi* population of *C. sloani.* Particularly when it is realized that many Mediterranean specimens match perfectly the descriptions of *dannevigi* with respect to the arrangement of small photophores, there seems no reason to consider *dannevigi* as anything more than a population of *C. sloani.*

TABLE II

Distribution of the number of light organs in the scale areas of the second row in three forms of *Chauliodus.* The body of the table shows the number of specimens of each species with the indicated percentage of second row organs containing two small photophores.

	Percentage of second row areas with two light organs										
Species	0	10	20	30	40	50	60	70	80	90	100
sloani	5	4	4	3	2	8	3	5	5	7	21
schmidti	9	6	1	1	0	3	0	0	1	0	0
dannevigi	2	3	3	1	0	0	5	0	0	1	1

In the scale areas of the third row, there are always two small photophores, except in *C. barbatus.* In that species there are three or more, arranged in a cluster of one slightly larger organ with two to many tiny organs. One specimen of *C. barbatus* examined by us appeared to have but two organs in about half of the third row scale areas, but as the skin of this fish was in very poor condition, this appearance may have been due to damage. The number of organs in the third row, then, will distinguish *C. barbatus* from all other species of the genus.

The scale areas of the fourth row each have two organs, as a general rule, in all species except *C. barbatus* and *C. macouni.* In these, the usual number is one. But in all forms, there is a considerable amount of variation. In *C. barbatus* and *C. macouni,* counts of fourth row organs vary from one to four, in *C. sloani* from one to three. We regard the number of organs in the fourth row scale areas as of only limited value in distinguishing the species of *Chauliodus.*

The number of teeth in the lower jaw has several times been used in the past in attempts to diagnose the species of *Chauliodus,* but it requires only a glance at Table III to see that the number of larger lower jaw teeth is of little taxonomic value. With such a range of variation as is shown here, the best that can be done is to say that there are differences in the average number of teeth in the lower jaw. *C. sloani* generally has six or seven teeth. *C. danae* most frequently has seven or eight teeth in the lower jaw, but there may be as few as five or as many as eleven. *C. schmidti* most often shows six teeth, *C. barbatus* and *C. macouni* six or seven, and the few specimens of *C. pammelas* that have been examined or reported in the literature all had only five teeth in the lower jaw.

TABLE III

Number of larger lower jaw teeth in various species of *Chauliodus*. The body of the table shows the number of specimens of each species. The data presented here include also tooth counts from Ege (1948).

	Number of Teeth						
Species	5	6	7	8	9	10	11
sloani	9	42	57	13	6		
danae	1	7	23	20	7	2	3
schmidti	5	23	7	3	1		
barbatus	0	7	5	1	1		
macouni	5	46	24	5	1		
pammelas	9						

Also in the lower jaw, the number of small denticles that may occur posteriorly, near the rictus, was used by Ege (1948) to separate *C. schmidti* and *C. pammelas*. Both our own observations and Ege's published data indicate that in *C. pammelas* the number of lower jaw denticles is a function of the size of the specimen. With this limitation in mind, it can be seen from Table IV that the number of lower jaw denticles can be a useful secondary character to distinguish these two species from each other, though it is of relatively little value amongst the others.

TABLE IV

Number of denticles in the lower jaw in *Chauliodus**

Species	0	1	2	3	4	5	6	7	8	9	10 or more
sloani	23	13	11	5	6	8	7	1	0	2	4
danae	27	3	4	9	6	1			**		
schmidti	17	1	1								
barbatus	5	3	5	3	1	1					
macouni	57	6	4	1	1						
pammelas		1				1	1		1		5

* Includes data published by Ege (1948) for 36 *C. sloani*, 7 *C. danae*, 4 *C. barbatus* and 4 *C. pammelas*.
** Regan and Trewavas (1929) give 3 to 8 denticles for *C. danae*.

The relative lengths of the first and second premaxillary teeth have been indicated as a distinguishing feature by which *C. macouni* might be separated from the other forms. The single specimen of *C. macouni* taken by the Dana had a remarkably short first premaxillary tooth, only 51.5 per cent of the length of the second. In all other species, with a few rare individual exceptions, the first premaxillary tooth is 60 per cent or more of the length of the second. This difference does not, unfortunately, hold good. All of the specimens of *C. macouni* examined by us have shown the first premaxillary tooth to be at least 60 per cent of the length of the second. We have found short first teeth only in *C. barbatus*. It may be of interest to note that all our specimens of *C. macouni* came from the northern part of the Pacific, whereas the Dana specimen was found in the tropics, west of the Galapagos Islands. It may be that the short teeth are somehow related to some characteristic of the Pacific Equatorial water mass, where *C. barbatus* also occurs. It may be mentioned here that the Dana specimen of *C. macouni* does not appear to have been mis-identified. Dr. Ege kindly re-examined the specimen, paying particular attention to the postocular photophore. The elongate, pointed shape of this organ and its location well behind the eye leave no doubt that it was correctly named.

Ege (1948: 138, 139) erected a new subspecies of *C. sloani* — *C. sloani secundus* — chiefly on the basis of slightly larger light organs in the scale areas of the first and fifth rows in his new form. He found that in *C. sloani* (*sensu stricto*) the small organs of the first row had a diameter of 4.0 to 4.8 per cent of the average length of the scale areas of the second row. In the same species, the length of the largest organ in the scale areas of the fifth row was 8.9 to 11.0 per cent of the average length of the same scale areas in one group, 11.4 to 11.7 per cent in another group. By contrast, the corresponding values for his new form were given as 6.8 per cent for the dorsal row and 12.5 per cent for the fifth row.

Examining specimens of *C. sloani* from the Atlantic, we observed an extremely wide range of variation in these two characters, leading us to make a detailed study of the matter. The length of the scale areas of the second row was measured on five consecutive scales on each specimen, beginning at the fifth scale behind the base of the ventral fins, and the average taken. The diameter of the appropriate light organ of the corresponding scales of the first and fifth rows was measured and expressed as a percentage of the average length of the scale areas of the second row. This was done with 64 specimens of *C. sloani* from the Atlantic, 12 specimens of *C. s. secundus* from the Indo-Pacific area, and 13 specimens of *C. sloani* from either the same localities as the *C. s. secundus* or from nearby stations. There was thus a total of 320 photophores from each row measured in the Atlantic sample, and 60 or 65 in each of the others.

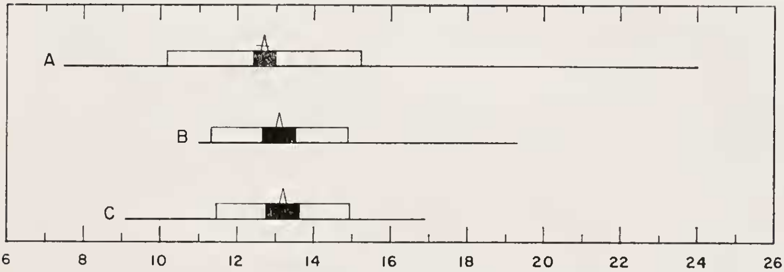

Figure 3. Distribution of the greatest diameter of the large light organ in the fifth row, expressed as percentages of the average diameter of the scale areas of the second row. A) *C. sloani* from the Atlantic. B) *C. sloani* from the Indo-Pacific. C) *C. sloani secundus.*

Figure 3 shows the mean, range, ± two standard errors, and ± one standard deviation for the photophores of the fifth scale row. There is obviously no significant difference in the value of the mean for the three distributions. The distribution of *C. s. secundus* is quite symmetrical, while the two samples of *C. sloani* are skewed to the left. What significance, if any, this may have we are not able to say.

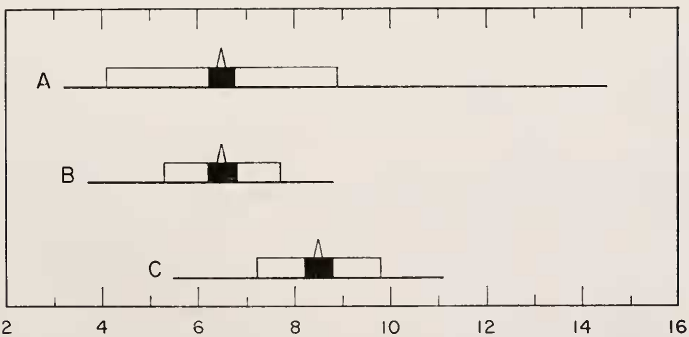

Figure 4. Distribution of the diameter of the light organ in scale areas of the first row, expressed as percentages of the average diameter of the scale areas of the second row. Lettering as in Figure 3.

A similar plot for the photophore of the first row is shown in Figure 4. Here there is an observable difference between the mean value for *C. s. secundus* and the two samples of *C. sloani*. However, the standard deviations of the distributions overlap each other to a considerable degree, indicating a good deal less than subspecific divergence.

The skewness of the Atlantic distribution, in particular, arouses curiosity. The actual distribution of the light organs, by size groups, has been plotted (Fig. 5), in order to obtain a clearer comparison of the three samples. The two Indo-Pacific samples look as though they were reasonably homogeneous, but the plot of the Atlantic sample gives the impression that it may be composed of two groups. One, the more numerous, has a mean value somewhere around five; the other, with a greater range, looks to have a mean in the neighborhood of nine. But we are still unable to find any means of separating out two groups from this single distribution. A scatter diagram of the size of the organ of the first row plotted against the size of the organ of the

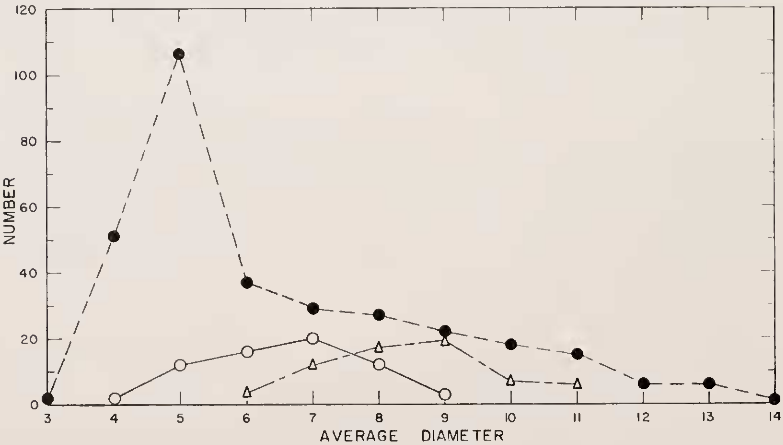

Figure 5. Frequency diagram of the distribution of the diameters of the first row organs. Solid circles — *C. sloani* from the Atlantic. Open circles — *C. sloani* from the Indo-Pacific. Triangles — *C. sloani secundus*.

fifth row (Fig. 6) shows in a rather striking fashion that there is actually no real reason for attempting to make such a separation. There appears to be a general increase in the size of one organ with the size of the other, but over so broad a base that it is difficult to draw any hard and fast conclusions on this matter.

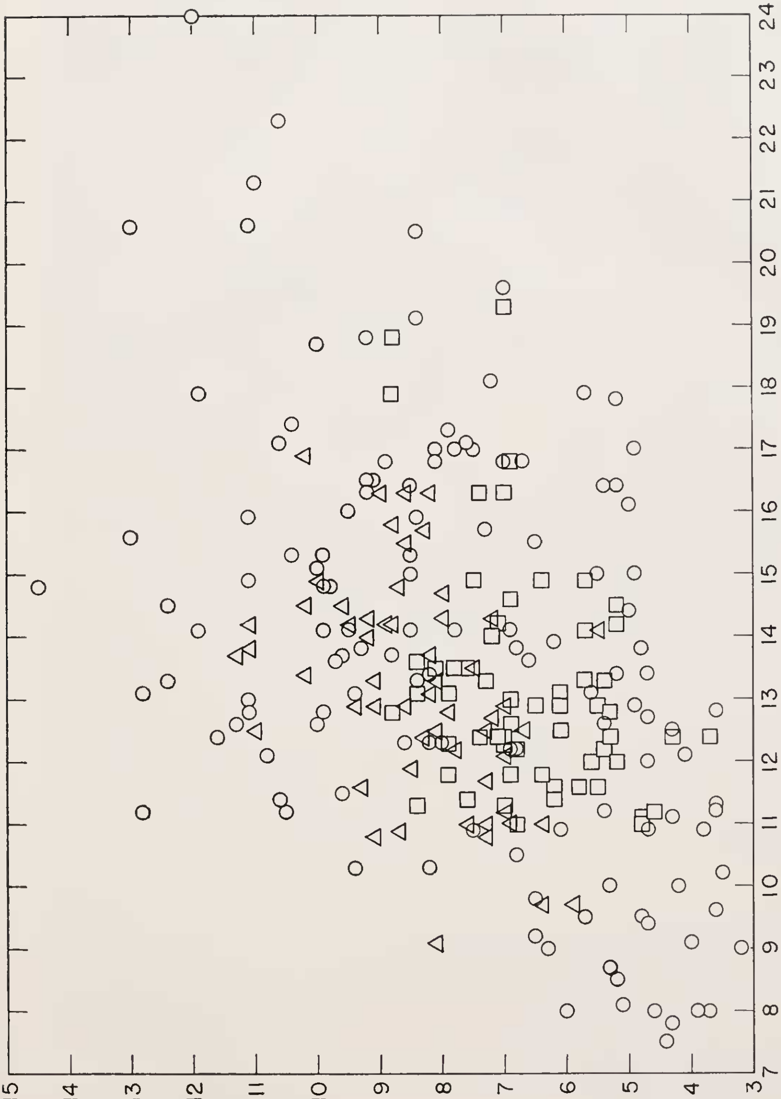

Figure 6. Scatter diagram of size of light organs of fifth scale row (abscissa) and of first row (ordinate) as percentages of average diameter of scales of second row. Circles — *C. sloani* from Atlantic. Squares — *C. sloani* from Indo-Pacific. Triangles — *C. sloani secundus.*

Further, the measurements of the organs of Indo-Pacific *C. sloani* and of *C. sloani secundus* fall entirely within the scatter of the Atlantic specimens of *C. sloani.* We are thus reinforced in our conclusion that *C. sloani secundus* should not be considered as a subspecies.

The number of serial photophores in the lateral and ventral series is an extremely valuable characteristic on which several species may be distinguished. In particular, *C. schmidti* and *C. pammelas* have much lower counts than any other species except *C. barbatus,* but they are readily distinguished from *C. barbatus* on other grounds. *C. pammelas,* with only 58 to 61 ventral organs and 38 to 39 lateral ones, falls completely outside the range of *C. sloani* for this character. For this reason we do not hesitate to consider *C. pammelas* as a species completely distinct from *C. sloani.* There seems to be no justification for maintaining *C. pammelas* as a subspecies of *C. sloani.* The matter of *C. schmidti* as a species or as a subspecies of *C. sloani* is not quite as clear cut, for there is some degree of overlap between the highest counts of *C. schmidti* and the lowest counts of *C. sloani.* Confining the discussion of the Atlantic forms of *C. sloani,* we find that this species has a total count of organs in the ventral row of 63 to 70. In the lateral row, the count is 42 to 48. For *C. schmidti,* the corresponding values are 60 to 63 and 38 to 42. But we must point out that in the ventral row counts, the number of *C. sloani* that overlap the range of *C. schmidti* is 3 out of a total of 298 specimens. (We have here included data on 197 specimens published by Ege (1948) and 101 specimens examined by us.) For the 54 specimens of *C. schmidti* reported by Ege, 14 had 63 photophores in the ventral row, 40 had 60 to 62. The coefficient of difference for the two distributions is 2.09, far above the usual subspecific level and indicating a much greater degree of differentiation. The same conclusion must be drawn from the graphic presentation of the statistics of these data, shown in Figure 7. The ranges of the two distributions meet at the value 63, but the two standard deviations are separated by a distance equal to 1.6 times larger. We feel completely justified, then, in raising *C. schmidti* to specific rank.

Two other items must be mentioned in this section. One of these is the shape and location of the postocular photophore, a characteristic which, as far as we know, has not previously been utilized in this group. In all species except *C. macouni,* this organ is more or less round and located generally somewhat anterior to a vertical through the posterior margin of the eye.

In *C. macouni,* however, the organ is generally triangular and pointed behind, sometimes notably elongate, and is placed posterior to the vertical through the hind border of the eye.

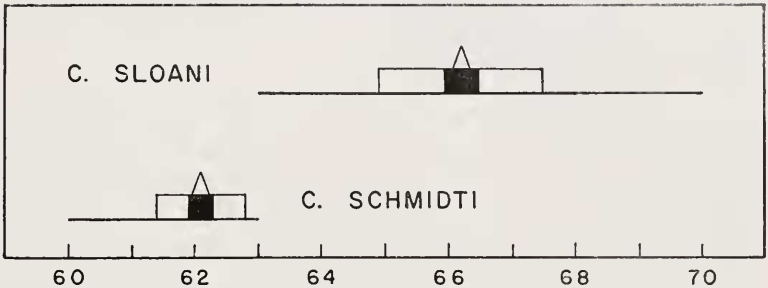

Figure 7. Distribution of the total number of serial photophores in the ventral row in two species of *Chauliodus.*

The other characteristic is the structure of the barbel. This was mentioned briefly by Regan and Trewavas (1929), but appears to have been ignored by most other workers. As Regan and Trewavas pointed out, the barbel of *C. sloani* is tapered and flexible, and disappears at a rather early age. This appears to be true also of *C. schmidti* and *C. pammelas.* In *C. danae* and *C. barbatus,* the barbel is stiff and compressed. In *C. danae,* the organ is quite straight, without expansions, and has degenerated in most specimens larger than 50 mm standard length. In *C. barbatus,* by contrast, the barbel bears a terminal, leaf-like expansion, and the whole organ is retained even in the largest specimens. In *C. macouni* the barbel resembles that of *C. sloani,* but is longer, stiffened basally, and does not degenerate.

DEFINITIONS

Two terms that have been and will be used in this paper require definition, as they are not ordinarily found in descriptions of fishes.

Scale areas. These are actually the scale pockets. (For a detailed description, see Morrow, Chauliodontidae, Fishes of the Western North Atlantic, Vol. 3.) The scales of *Chauliodus* are large and fairly heavy. However, they are extremely deciduous, and appear also to dissolve readily in the ordinary preserving fluids. In addition, the skin is, in life, covered with a thick layer of mucus which makes it very difficult to distinguish the scales themselves. Each scale pocket is outlined by a pigment pattern, so that even after the scales are lost, the areas can often be distinguished with a fair degree of ease and accuracy. In the terminology used here, the most dorsal row of scales is called the first row. The scales of this row are much smaller than the others, and are often almost impossible to see. The most ventral row of scales is termed the fifth row.

SM organs. These are the small light organs lying in the area between the lateral and ventral rows of serial light organs. The arrangement of these small organs is here indicated by a numerical formula showing the number of small, unpigmented organs at each end and the number of somewhat larger pigmented organs in the middle of the series between adjacent pairs of large, serial photophores. Thus, 1+3+0 would indicate one small unpigmented organ at the anterior end of the series, three larger, pigmented organs in the middle part, and no organ at the posterior end.

All descriptions of scale areas and SM organs refer to the part of the body beginning four or five scales behind the bases of the ventral fins and extending posteriorly for about ten scales.

Family CHAULIODONTIDAE

Characters. Body long, slender, compressed, covered by five longitudinal rows of large scales. Scales deciduous, their location often marked only by pigment pattern. Ventral fins before middle of body measured from snout, of seven or eight rays. Dorsal fin in anterior third of body, far in advance of anal fin, its first ray much produced into a long filament, terminating in a small flap. Adipose dorsal and anal fins present. Anal fin far posterior, close to caudal.

Premaxillaries not protractile. Well developed epiotics present beside supraoccipital. Parietals minute. First few vertebrae without centra, the notochord enclosed in a sheath, first vertebra with a large single parapophysis below, and long paired laminae above representing neural arch. The enlargement of this vertebra, together with the acentrous nature of the ones behind it, is related to throwing back the head in order to open the mouth in feeding (Tchernavin, 1953). The remainder of the skeleton is much like that of the Astronesthidae, and is but poorly ossified.

Snout short, more or less equal to eye. Nostrils large, immediately before eyes, the complex olfactory laminae exposed. Interorbital less than eye, with a prominent bony ridge above each eye. Teeth of premaxillary and mandible rigid, large to enormous, fang-like. Mandible with none to many tiny denticles near rictus. Maxillary with numerous fine teeth on posterior half to two-thirds of its ventral margin, entering posterior portion of gape. Vomer toothless. Palatines with a few teeth anteriorly, followed by a space, then several minute teeth. Operculum small. Four gills, a slit behind the fourth. Gill arches armed with teeth, but no true gill rakers. Mental barbel generally short and simple, becoming much reduced or absent in juveniles and adults of some species, retained in others.

Postocular luminous organ present, below and just before or somewhat behind posterior margin of eye, another organ imbedded in skin immediately before eye. Small photophores present in each scale area. A row of large light organs present on each side of body, beginning immediately behind gill opening and ending above or nearly above anterior end of anal fin. Another row of large photophores below these, beginning at anterior end of isthmus and ending at caudal base. Between the two rows of large organs is a wavy row of small ones (here termed SM organs), whose pattern more or less repeats itself between each pair of large serial organs, and appears to be diagnostic for some species. Groups of small organs present on mid-ventral line between the two ventral rows of large photophores. Light organs present on branchiostegal membranes, between rays.

Miscellaneous anatomy. The internal anatomy of the major systems is typical of pelagic teleosts, with minor adaptations in the digestive system which are presumably related to the availability of food in the mid-depths. It has been examined in detail by Haffner (1952a), whence most of the following account has been derived.

The most prominent feature of the digestive tract is the long, sac-like stomach. Apparently it is not particularly distensible, but achieves its capacity through its length. As with other pelagic fishes, the esophagus, intestine and pyloric caeca join the stomach at its anterior end.

The esophagus is muscular, lined with short columnar epithelial cells, some of which, in the anterior portion, have a short, curved spine at their free end. The spines disappear in the posterior portion of the esophagus, and their function is unknown. In the anterior portion of the stomach, the mucosal lining is thrown into folds, with each fold bearing a lymph nodule at its tip. The pyloric caeca are thin-walled, and the mucosa and submucosa are much folded, resulting in the division of each caecum into numerous small compartments. Haffner suggested that the compartments were so small as to prevent the entrance of food into them, and hazarded that the caeca might be secretory in function. The intestine, arising on the ventral side of the stomach at its anterior end, extends straight back to the anus with no change in diameter.

The kidneys are long and narrow, extending the full length of the body cavity, and appear to be aglomerular. The urinary bladder opens through a pore behind the opening of the genital duct. The gonads resemble the kidneys in gross appearance, but do not reach as far posteriorly. The genital ducts empty through a pore between the anus and the urinary pore.

The swim bladder, according to Marshall (personal communication of information in press), is either absent, or degenerates completely at a very early stage.

The microscopic structure of the photophores has been the subject of several investigations, (Chiarini, 1900; Brauer, 1908; Haffner, 1952a), with the result that they have been thoroughly described and illustrated. There are four types, the simplest being merely a small, spherical mass of radially-arranged columnar cells, without pigment layer, lens, or reflector. The next form, of which the sub-ocular photophore is typical, also lacks lens and reflector, but is provided with a layer of dark pigment covering about ¾ of its surface. Its structure resembles that of the simplest type, except that instead of a lumen, the center of the organ is filled with what Brauer interpreted as coils of cells, but which Haffner thought could be explained more readily as the cut ends of radially-arranged columnar cells. The more complex organs, consisting of light-producing elements, pigment layer, lens and reflector, are of two types, the bowl and cup-shaped organs, and the bell-shaped organs. The former have a single, the latter a double lens.

The photophores were early thought to be equipped with nerve fibers, but later workers have interpreted the observed structures as blood vessels, indicating that the luminescence of the photophores is under hormonal rather than direct nervous control.

Range. The several species of *Chauliodus,* the only genus of the family, are found in nearly all parts of the oceans, having been taken throughout the North Atlantic and Mediterranean, at various localities in the South Atlantic, and in the Pacific and Indian oceans. In general, the range lies between 50°N and 40°S, although *C. macouni* is commonly found in the Gulf of Alaska to

60°N, and there are few records of *C. sloani* in the Atlantic between 55°N and 65°N.

In their vertical distribution, the members of this group may be found as close to the surface as 20 meters, and down to depths as great as 2,800 meters. Several species appear to have different depth preferences, and all appear to be more or less limited in their distribution by certain physical and chemical characteristics of the water masses. In general, larger individuals, and also species reaching larger sizes, tend to live at greater depths than do the smaller ones.

Genus CHAULIODUS Bloch and Schneider, 1801

Chauliodus Bloch and Schneider, Systema Ichthyologiae, Berlin, 1801: 430; type species *C. sloani* Bloch and Schneider, 1801, by monotypy.

Generic Synonym:

Leptodes Swainson, Nat. Hist. Classification Fishes, Amphibians and Reptiles. London, 1839: 298; type species *L. sloanii* (Bloch and Schneider).

Generic characters. As for the family.

Size and habits. The various species included in *Chauliodus* are of no more than moderate size. *C. sloani* has been recorded at a length (standard or total?) of 350 mm (Zahl, 1953), but the vast majority of individuals do not appear to exceed about 300 mm standard length. *C. danae*, in particular, does not appear to reach more than about half this length.

The habits of this group, are, of course, unknown from direct observation, but examination of stomachs of preserved individuals has shown them to be carnivores, feeding on other fishes and on crustaceans. Tchernavin (1953) has deduced the detailed mechanics of their feeding actions from a study and dissection of *C. sloani.* Larval development of *C. sloani* has been described, but that of other species remains unknown. (For a résumé, with many references, of current knowledge of larval development in *Chauliodus,* see Morrow, Fishes of the Western North Atlantic, vol. 3.)

Species. All told, some 14 names, which do not include combinations, have been applied to the members of the genus *Chauliodus,* but no one has ever attempted to accept all fourteen as valid. The first attempt to list the species seems to have been that of Garman (1899), who recognized five, but made no indication of his thoughts on the remaining three which had been described at that time. Brauer (1906) considered the matter in more detail and accepted the same five species. He also pointed out that *C. setinotus* Bloch and Schneider and *C. schneideri* Risso were synonyms of *C. sloani* Bloch and Schneider. Regan and Trewavas (1929) gave detailed descriptions of their material of three species and suggested that *C. dannevigi* and *C. macouni* might be synonyms of *C. sloani* and *C. barbatus,* respectively. Finally, Ege (1948) accepted only *C. sloani*, *C. danae* and *C. barbatus* as full species, reducing *pammelas, dannevigi* and *macouni* to subspecies of *sloani* and describing two new subspecies, *schmidti* and *secundus.* Thus, he considered that there were three species, one of which was split into six subspecies, for a total of eight forms.

In the present paper, we recognize six species. The subspecies of Ege we feel should either be raised to specific rank or synonymized altogether, as has already been pointed out in the section on species criteria.

Key to Species

1a. Postocular photophore elongate, the exposed luminous portion triangular or at least pointed behind; the organ itself located below or behind a vertical through posterior edge of eye.

C. macouni Bean
Gulf of Alaska, North Pacific Ocean

1b. Postocular photophore round or nearly so, exposed luminous portion never triangular or pointed behind; the organ itself located below or before a vertical through posterior edge of eye.

2a. Serial photophores of lateral series ventral to scale areas of fourth row. Majority of scale areas of 3rd row generally with a cluster of 3 or more small light organs.

C. barbatus Garman
Gulf of Panama, tropical Pacific

2b. Serial photophores of lateral series below scale areas of fifth row. Scale areas of 3rd row with not more than 2 small light organs.

3a. Dorsal origin over 9th to 12th OV photophore.

4a. Posterior unpigmented organ of each SM series generally absent, or at least much reduced. SM formula generally 1+2+0. Chin barbel (when present) short, stiff, compressed,

absent in most specimens larger than ca 50 mm.
C. danae Regan and Trewavas
North and South Atlantic Ocean.

4b. Posterior organ of each SM series nearly as large as the central organs. SM formula generally 1+3+1 or 1+4+0. Barbel tapered, slender, flexible, generally present in most specimens up to ca 100 mm.
C. sloani Bloch and Schneider
(some Indo-Pacific variants)

3b. Dorsal origin over 5th to 8th OV photophore.

5a. Total ventral photophores 64 to 72, rarely 62 or 63. Total lateral photophores 43 to 48, rarely 42.
C. sloani Bloch and Schneider
Atlantic, Pacific, Indian oceans, Mediterranean Sea.

5b. Total ventral photophores 58 to 63. Total lateral photophores 38 to 42.

6a. SM series with 3, sometimes 4 larger pigmented organs in each series. Total ventral organs 58 to 61, total lateral organs 38 to 39.
C. pammelas Alcock
Northern Indian Ocean

6b. SM organs with only 2 larger pigmented organs in each series. Total ventral organs 60 to 63, total lateral organs 38 to 42.
C. schmidti Ege
Eastern Atlantic Ocean

Chauliodus barbatus Garman, 1899

Study material. Nineteen specimens, 74 to 183 mm standard length, from the Gulf of Panama, Galapagos Islands and off Peru.

Distinctive characters. C. barbatus is particularly characterised by the following: Serial photophores of the lateral series located on verticals passing approximately through the centers of the scale areas of the fourth row; barbel stiff, compressed, expanded at tip, present at all stages; dorsal origin over 8th to 11th OV photophore; total lateral photophores 38-41; total ventral photophores 59-63.

Description. Proportional measurements of the study material given as average percentages of standard length except as indicated otherwise, with the range of variation shown in parentheses.

Body: depth 9.9 (7.1-14.8).

Head: 15.3 (13.5-16.5).

Eye: 3.1 (2.6-3.4); 20.1% of head (17.0%-22.3% of head).

Snout: 3.5 (3.1-4.1); 22.6% of head (19.5%-26.0% of head).

Distance from snout: to origin of dorsal fin 27.0 (25.1-29.0); to origin of anal fin 81.7 (79.0-83.1); to origin of ventral fin 41.9 (40.5-44.1).

Pre-anal length without head: 66.5 (63-69).

Dorsal fin: rays 6.

Anal fin: rays 10-13.

Pectoral fin: rays 10-13.

Ventral fin: rays 7.

Vertebrae: 51-55, most often 53.

Serial photophores: Ventral row: IP 9-11; PV 16-19; VAV 22-24; AC 10-11; Total 59-63. Lateral row: OV 17-18; VAL 20-23; Total 38-41.

Body elongate, slender, compressed, the depth averaging about 10 per cent of the standard length, slightly deeper than in other species. Barbel present at all stages, short, stiff, compressed, terminally expanded. Edges of expanded part usually crenate (Fig. 8).

Head about 1/7 of standard length, with prominent bony ridges above each eye. Eye round, about 1/5 of head. Snout slightly longer than eye diameter. Subocular organ present below anterior part of eye, deeply embedded in skin. Postocular organ more or less round, located below posterior part of eye.

Mouth large, jaws almost equal to head length. Premaxillaries with four teeth, second tooth longest, third tooth longer than (rarely equal to) fourth. Many small oblique teeth on maxillary. Mandible with 6 to 9 larger teeth, and up to 5 tiny denticles posteriorly, near corner of mouth.

Origins of pectoral fins low on body, just anterior to posterior edge of opercular flap when head is in normal position. Fins of 10 to 13 rays. Ventral fins of 7 rays, their origins before middle of standard length. Dorsal fin of 6 rays, its origin over the 8th to 11th OV photophore. Anal fin far behind dorsal, close to caudal, with 10 to 13 rays, most often 12 or 13. Caudal fin forked.

Scale areas of the second row almost always, and of the fourth row usually, with only one small light organ. Areas of the third row with a cluster of three or more small organs, usually one slightly larger and two to many rather minute ones. Serial photophores lying below scales of fourth row, scales of fifth row extending ventrally between the organs of the lateral row. SM organs small, usually five to seven of about equal size in each section.

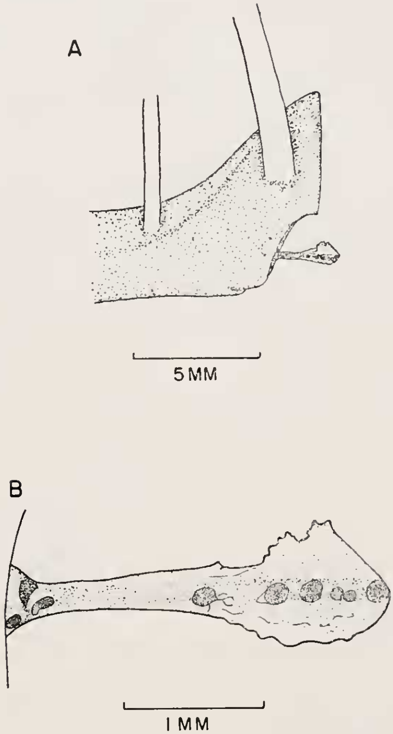

Figure 8. Barbel of *C. barbatus* Garman, drawn from Galathea specimen No. 15. A) Showing relation to lower jaw. B) The barbel itself, much enlarged.

Size. The largest specimen examined was 183 mm in standard length. It seems likely that this species does not much exceed 200 mm.

Relationships. *C. barbatus* clearly represents an individual offshoot within the genus. Although the stiff compressed barbel suggests affinities with *C. danae,* and the retention of the barbel throughout life is found also in *C. macouni,* the arrangement of the serial light organs below the fourth, rather than the fifth, scale row, the presence of a group of organs rather than a pair in the areas of the third row, and the increased number and reduced size of the SM organs all indicate that *C. barbatus* is the most divergent species of the genus.

Range. Known only from the eastern part of the Pacific Equatorial water mass, from the coast of Peru north to the Gulf of Panama (possibly as far north as Central America) and westward to about 100°W. In depth, *C. barbatus* has been taken down to about 1200 fathoms, but the majority of records seem to be from between 500 and 700 fathoms.

Synonyms and references:

Chauliodus barbatus Garman, Mem. Mus. Comp. Zool. Harvard, *24,* 1899: 271-273, Pl. K, figs. 2, 2a (type descr., illus., type localities 6°22′20″N, 81°52′W, 465 fath., and 3°09′N, 82°08′W, 1132 fath., type specimens, Harvard Mus. Comp. Zool., Nos. 28489 and 28490); Brauer, Ergebn. Deutsch. Tiefsee-Exped. "Valdivia", *15*, Syst. Teil, 1906: 38-40 (comparison species); Gilbert, Proc. U.S. Nat. Mus., *48,* 1915: 321 (name); McCulloch, Biol. Res. "Endeavour", 1916, *4* (4): 181 (name); Regan and Trewavas, Dana Rept., No. 5, 1929: 38-39 (descr., Gulf of Panama); Jordan, Evermann and Clark, Rep. U.S. Comm. Fish., (1928) 1930, App. X: 71 (name); Ege, Dana Rept., No. 31, 1948: 148 pp. (descr., synonymy, zoogeogr.); Haffner, Syst. Zool., *1* (3), 1952: 114 (name, Gulf of Panama to Galapagos); Marshall, Aspects of Deep Sea Biology, New York, 1954: 65 (name).

Chauliodus danae Regan and Trewavas, 1929

Study material. Seventy specimens 37 to 133 mm standard length, from the Caribbean Sea and North Atlantic Ocean.

Distinctive characters. The posterior position of the dorsal origin, the short stiff barbel of the young, and the reduced SM organs serve to distinguish *C. danae.*

Description. Proportional measurements of the study material expressed as mean percentages of standard length except as noted otherwise, with the range of variation shown in parentheses. Data from other authors in brackets.

Body: depth 7.7 (4.7-11.9).

Head: 12.9 (11.9-14.3).

Eye: 3.3 (2.2-4.9); 26.9% of head (17.7%-43.2% of head).

Snout: 2.8 (1.7-3.7); 22.3% of head (16.7%-28.8% of head).

Distance from snout: to origin of dorsal fin 28.1 (25.9-32.3); to origin of anal fin 85.7 (83.5-88.7); to origin of ventral fin 42.7 (39.7-45.7).
Pre-anal length without head: 73 (71-77).
Dorsal fin: rays 6.
Anal fin: rays 10-12.
Pectoral fin: rays 12-13 [14].
Ventral fin: rays 7.
Vertebrae: 51-57, most often 53-55.
Serial photophores: Ventral row: IP 9-10; PV[17]18-21; VAV[22]23-26; AC 8-10; Total 61-65. Lateral row: OV 17-20; VAL 22-25; Total 40-44.

Body compressed, elongate, slender, the depth averaging only about 1/15 of the standard length. Barbel present only in young (less than ca 50 to 55 mm SL), compressed, straight, with a stiffening axial rod, reduced to a small triangular stump in adults. (Fig. 9.)

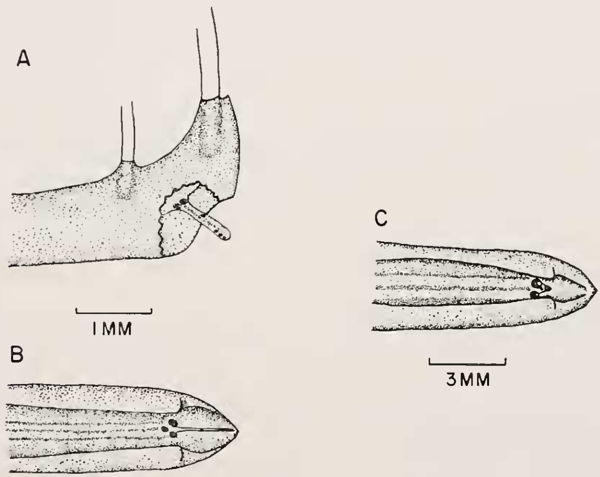

Figure 9. Barbels of *C. danae.* A) Lateral view, with part of lower jaw cut away, of barbel of a 50 mm specimen (Bingham Oceanogr. Coll., No. 2938). B) Ventral view of same. C) Ventral view of barbel of a 114 mm specimen (Bingham Oceanogr. Coll., No. 2935) showing reduction in adult.

Head averaging about 1/8 of standard length, bony ridges present above eyes. Eye round, its diameter quite variable, generally somewhat larger in males than in females (Regan and Trewavas, 1929: 34). Snout slightly shorter than eye diameter. Subocular organ present below front of eye, deeply embedded. Postocular organ round, below posterior part of eye.

Mouth large, jaws almost equal to head length. Premaxillaries with four teeth, second longest, third tooth shorter than (rarely about equal to) fourth. Many small, oblique teeth on maxillary. Mandible with 5 to 11 teeth, generally 7 or 8, with up to 8 denticles posteriorly near corner of mouth (see Table IV).

Pectoral fins with 12 to 14 rays, their origins low on body, about below posterior edge of opercular flap. Ventral fins with 7 rays, their origins before middle of standard length. Dorsal fin of 6 rays, its origin generally over 9th to 11th OV photophore, rarely 8th or 12th. Anal fin far behind dorsal, close to caudal, with 10 to 12 rays. Caudal fin forked.

Scale areas generally clearly marked by pigment patterns, each area with one or more small light organs, those of the third row with not more than two photophores. Areas of second and fourth rows each with two organs. Serial photophores lying below scales of fifth row. SM organs generally with the posterior organ of each section absent or at least much reduced, the SM formula 1+2+0.

Size. The largest specimen seen by us was 133 mm in standard length. According to Regan and Trewavas (1929: 35), the maximum size is about 140 mm.

Relationships. Closest to *C. sloani*, from which it differs chiefly in the structure of the barbel, the posterior placement of the dorsal fin, the reduced SM organs and the somewhat lower number of serial photophores.

Range. The majority of the known specimens of *C. danae* have come from a broad east-west belt across the North Atlantic, extending roughly from 20°N to 40°N. However, other specimens have been recorded from the South Atlantic, as far as 33°53′45″S, and from as far north as 51°N. In addition, the species has also been recorded from the area along the eastern edge of the Caribbean Sea and from the Yucatan Channel, west of Cuba. Within these areas, it appears that *C. danae* is restricted to water in which the degree of oxygen saturation is at least 50 per cent. Depthwise, *C. danae* has been recorded as far down as about 3500 meters (7000 meters of wire out), but the majority of specimens appear to be taken in the upper 500 meters of water.

Synonyms and References:

Chauliodus danae Regan and Trewavas, Dana Rept., No. 5, 1929; 34-38, pl. VII (type descr., type locality 13°03′N, 59°50′W, 300 m wire, type specimen Dana Coll. No. St. 1182); Norman, Discovery Rept., *2*, 1930: 308 (South Atlantic); Borodin, Bull. Mus. Comp. Zool. Harvard, *72* (3), 1931: 64 (Bermuda); Fowler, Bull. Amer. Mus. Nat. Hist., *70* (2), 1936: 1199-1200 (name); Beebe, Zoologica, N.Y., *22* (14), 1937: 201 (Bermuda, 300-1,000 fath.); Parr, Bull. Bingham Oceanogr. Coll., *3* (7), 1937; 58 (Bahamas, Bermuda); Bertin, Bull. Mus. Hist. Nat. Paris, (2) *11*, 1939: 382 (name); Nybelin, Göteborg Vetensk. Samh. Handl., (B) *5* (16), 1948: 30 (N.E. Atlantic); Ege, Dana Rept., No. 31, 1948: 1-148 (classification, phylogeny, zoogeography); Haffner, Systematic Zool., *1*, (3), 1952: 112-113 (zoogeography); Grey, Fieldiana:Zool., *37*, 1955: 277-278 (Bermuda, stomach contents, eggs); Koefoed, Rep. Sars N. Atlantic Deep Sea Exped., *4* (2) (5), 1956: 19-20 (N. Atlantic, table of measurements).

Chauliodus atlantis (partim) Barbour, Proc. New Engl. Zool. Cl., *19*, 1942: 46.

Probable synonym:

Chauliodus pammelas Pappenheim, Deutsch. Sudpolar Exped., *15*, Zool. *7*, 1914: 167 (N. Atlantic).

Not *Chauliodus danae* Phillipps, Rec. Dominion Mus., *1* (1), 1942: 53-54 (Cook Strait).

Chauliodus macouni Bean, 1891

Study material. Ninety-three specimens, 30 to 182 mm standard length, from the northeastern Pacific Ocean and south of Japan.

Distinctive characters. The generally triangular form of the postocular organ, and its location behind and below the eye provide absolutely distinctive characters by which to distinguish *C. macouni* from all other species of the genus.

Description. Proportional measurements of the study material expressed as average percentages of standard length, unless indicated otherwise, with the range of variation shown in parentheses. Data in brackets from other authors.

Body: depth 8.1 (6.7-10.1).

Head: 15.8 (13.2-17.2).

Eye: 3.3 (2.8-4.0); 20.8% of head (16.9%-28.1% of head) [30.3].

Snout: 3.8 (2.8-4.5); 24.4% of head (17.7%-28.7% of head) [30.3].
Distance from snout: to origin of dorsal fin 24.9 (22.2-27.8); to origin of anal fin 83.3 (80.9-84.7) [76.8-90.8]; to origin of ventral fin 41.3 (37.6-44.5) [35.7-47.5].
Pre-anal length without head: 68 (64-72).
Dorsal fin: rays 6 [rarely 7].
Anal fin: rays 10-13.
Pectoral fin: rays 10-13.
Ventral fin: rays 7 [rarely 8].
Vertebrae: 56-62.
Branchiostegal rays: 16-20 [21].
Serial photophores: Ventral row: IP 9-12; PV 17-21; VAV 26-29 [30]; AC 10-13; Total 66-69. Lateral row: OV 17-20; VAL 24-28 [29]; Total 43-46.

Body slender, elongate, compressed, its depth averaging about 1/12 of the standard length. Barbel rather longer than in other species, tapered, stiff basally but flexible near tip, present at all stages (Fig. 10).

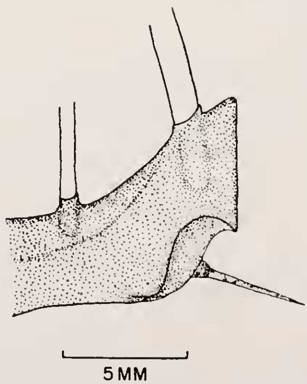

Figure 10. Barbel of *C. macouni*. Drawn from Bingham Oceanogr. Coll., No. 1287, 159 mm standard length.

Head almost 1/6 of standard length, with the usual bony ridges above eyes. Eye round, its horizontal diameter averaging about 1/5 of head. Snout generally a little longer than eye. Subocular organ present below and before eye, deeply embedded. Postocular organ located generally behind a vertical through posterior margin of eye, the organ itself distinctly elongate, the exposed luminous surface generally markedly triangular or at least pointed behind, sometimes notably attenuate.

Mouth large, jaws almost equal to head. Premaxillaries with four teeth, second largest, third tooth longer than (rarely equal to) fourth. Many small, oblique teeth on posterior part of maxillary, which enters gape. Mandible with five to nine larger teeth, generally six or seven. Usually no denticles on posterior part of mandible, but sometimes as many as four present. (See Table IV.)

Pectoral fins arising low on body, below posterior edge of opercular flap, of 10 to 13 rays. Ventral fins of 7 rays, arising well before middle of standard length. Dorsal origin over 6th to 9th OV photophore, average predorsal distance about ¼ of standard length. Anal fin far behind dorsal, close to caudal, of 10 to 13 rays. Caudal fin forked.

Body with five longitudinal rows of scales, large serial photophores of lateral row lying below scales of fifth row. Scale areas of second row generally with only a single light organ, those of third row with two, those of fourth row usually with one photophore. SM organs generally 0+2+1, but showing considerable variation, sometimes 1+4+0, the latter formula found in the type specimen and a few others.

Size. The largest specimen examined, at 182 mm SL, appears to be the longest on record, suggesting that this species may not ever grow to much over about 200 mm SL.

Relationships. C. macouni appears to be closer to *C. sloani* than to any other species in the genus, although the long third tooth of the premaxillary and the permanent nature of the chin barbel indicate affinities with the stock from which *C. barbatus* must have arisen.

Range. The vast majority of records of *C. macouni* have come from the subarctic Pacific water mass and the intermediate water to the west of it, with a few from the transitional region that extends south along the California coast. There are a few records from other masses, e.g., one from the Pacific Equatorial Water near the Galapagos Islands and another from south of Japan in the border region between Intermediate and Western North Pacific Central Water, but it is quite possible that these were strays and that these records do not really represent the normal extension of the range. Present information, then, suggests that the ordinary range of *C. macouni* includes the southern part of the Bering Sea, southeastward through the Gulf of

Alaska at least as far as the southern part of California, and westward about to Sakhalin, possibly as far as Japan.

Synonyms and references:

Chauliodus macouni Bean, Proc. U.S. Nat. Mus., *13*, (1890) 1891: 44 (type descr., type locality 51°23'N, 130°34'W, 876 fath., type specimen U.S. Nat. Mus., No. 45372); Gilbert, Rept. U.S. Comm. Fish., (1893) 1895: 402 (off Oregon, Alaska); Goode and Bean, Oceanic Ichthyol., Washington, 1895: 513 (name); Jordan and Evermann, Bull. U.S. Nat. Mus., *47*, 1896: 585 (descr.); Garman, Mem. Mus. Comp. Zool. Harvard, *24*, 1899: 274 (name, meristic counts); Brauer, Ergebn. Deutsche Tiefsee-Exped. "Valdivia", *15* Syst. Teil., 1906: 38-40 (comparison other spp.); Gilbert, Proc. U.S. Nat. Mus., *48*, 1915: 321-322 (descr., comparison other spp., So. Calif.); McCulloch, Biol. Res. "Endeavour", *4* (4), 1916: 181 (name); Jordan, Evermann and Clark, Rep. U.S. Comm. Fish., (1928) 1930, App. X: 71 (name); Chapman, Occ. Pap. B. C. Prov. Mus., No. 2, 1940: 5-11 (distrib., descr., comparison *C. barbatus*); Clemens and Wilby, Bull. Fish. Res. Bd. Canada, *68*, 1946: 108-109 (descr., illus., food, range); Barraclough, Copeia, 1950 (3): 241-242 (inshore record, Brit. Columbia); Copeia, 1954 (1): 75-76 (same).

Chauliodus emmelas Jordan and Starks, Bull. U.S. Fish. Comm., *22*, 1904: 579 (type descr., type locality Sagami Bay, Japan, 120-265 fath., type specimen U.S. Nat. Mus., No. 51464); McCulloch, Biol. Res. "Endeavour", *4* (4), 1916: 181 (name).

Chauliodus sloanei macouni Ege, Dana Rept., No. 31, 1948: 148 pp. (descr., near Galapagos Is.); Haffner, Systematic Zool., *1* (3), 1952: 114, 132 (name, range).

Chauliodus pammelas Alcock, 1892

Study material. Seven specimens, 25 to 159 mm standard length, from the Gulf of Aden, Arabian Sea and near the Maldive Islands.

Distinctive characters. *C. pammelas* is set off primarily by the low number of serial photophores, the forward position of the dorsal fin, and the 3 or 4 pigmented SM organs.

Description. Proportional measurements of the study material as mean percentages of standard length, unless indicated otherwise, with range of variation in parentheses.

Body: depth 8.5 (7.2-9.5).

Head: 15.1 (14.0-16.5).

Eye: 3.3 (2.8-4.4); 21.6% of head (19.1%-23.4% of head).

Snout: 3.5 (3.1-4.4); 22.3% of head (20.6%-25.1% of head).

Distance from snout: to origin of dorsal fin 23.2 (21.5-26.7); to origin of anal fin 83.5 (82.5-84.5); to origin of ventral fin 43.8 (41.5-45.3).

Pre-anal length without head: 67.9 (63-70).

Dorsal fin: rays 6.

Anal fin: rays 12-13.

Ventral fin: rays 7.

Pectoral fin: rays 12-14.

Vertebrae: 50-53.

Branchiostegal rays: 17-20.

Serial photophores: Ventral row: IP 10; PV 17-19; VAV 21-23; AC 9-11; Total 58-61. Lateral row: OV 18-19; VAL 19-22. Total 38-39.

Body, slender, elongate, compressed, depth about 1/12 of standard length. Chin barbel reduced to triangular stump in study material.

Head 1/6 to 1/7 of standard length, a bony ridge above each eye. Eye round, average diameter a little more than 1/5 of head, averaging slightly less than snout length. Snout short, less than ¼ of head. Subocular organ present below front of eye, deeply embedded in skin. Postocular organ round, below eye, before a vertical through posterior margin of eye.

Mouth large, jaws nearly equal to head length. Premaxillaries with four teeth, second tooth longest, fourth tooth longer than third. Maxillaries with numerous small, oblique denticles on posterior part of ventral margin, entering gape. Mandible with five teeth, and up to 17, perhaps more, tiny denticles near corner of mouth. The number of denticles appears to be a function of the size of the individual, increasing as the fish grows.

Origins of pectoral fins low on body, about below posterior edge of opercular flap. Fins of 12 to 14 rays. Ventral origins before middle of standard length, close together at mid-ventral line. Dorsal fin arising over 6th or 7th lateral OV photophore, pre-dorsal distance 21.5 to 26.7 per cent of standard length. Anal fin far behind dorsal, close to caudal, with 12 or 13 rays. Caudal fin forked.

Body with five longitudinal rows of scales, the scale areas marked off by pigment patterns. Second row with one or (more often) two small organs in each scale area. Each area of third row with only two small light organs, areas of fourth row also with two organs. Serial photophores ventral to scale areas of fifth row. SM organs moderate, SM formula usually 0+3+1, sometimes 0+4+0.

Size. The type specimen, described by Alcock (1892: 355) as "10 inches long," is the largest of which we have found a record.

Relationships. C. pammelas is obviously derived from the *sloani* stock, and appears to occupy a position close to *C. schmidti* of the Atlantic, which it resembles, especially in the low number of serial photophores. Whether the ecological positions are similar is not known.

Range. This species has been recorded from the Gulf of Aden, eastwards across the Arabian Sea to the Maldive-Laccadive area, south and west of Ceylon, in the Bay of Bengal and southwest of the Nicobar Islands, and once from the Flores Sea. The last is the only record ascribed to this species south of the equator. The depth range apparently goes to something on the order of 2500 meters, with several other positive records between 500 and 1000 meters, approximately. Unfortunately, this species is not particularly abundant in collections, and its distribution is therefore not well known.

Synonyms and references:

Chauliodus pammelas Alcock, Ann. Mag. Nat. Hist., (6) *10,* 1892: 355 (type descr., type locality Laccadive Sea, 8°49′N, 73°18′45″E, 1370 fath., type specimen Indian Mus. No. 13183); Goode and Bean, Oceanic Ichthyol., Washington, 1895: 96 (name); Alcock, Descr. Cat. Indian Deep Sea Fishes, Calcutta, 1899: 145 (not seen); Illus. Zool. "Investigator," 1900: Pl. 30, fig. 4 (not seen); Brauer, Ergebn. Deutsche Tiefsee-Exped. "Valdivia", *15* Syst. Teil, 1906: 38-42 (comparison other spp.); 42-43 (descr.); Weber and de Beaufort, Fishes Indo-Austral. Archipel., Leiden, vol. 2, 1913: 110-111 (name); McCulloch, Biol. Res. "Endeavour", *4* (4), 1916: 181 (name); Regan and Trewavas, Dana Rept., No. 5, 1929: 31 (name); Fowler, Bull. Amer. Mus. Nat. Hist., *70* (1), 1936: 221 (name); Norman, Sci. Rept. John Murray Exped., *7* (1), 1939: 21-22 (descr., distrib.).

Chauliodus sloanci pammelas Ege, Dana Rept., No. 31, 1948: 148 pp., (descr., synonymy, zoogeogr.); Haffner, Systematic Zool., *1* (1), 1952: 113-133 (zoogeogr.).

Chauliodus sloani pammelas, Marshall, Aspects Deep Sea Biol., N.Y., 1954: 66 (name).
Probable synonym:
Chauliodus sloanii (partim), Alcock, Descr. Cat. Indian Deep Sea Fishes, Calcutta, 1899: 144 (not seen).
Not *Chauliodus pammelas* Pappenheim, Deutsche Südpolar Exped., *15*, Zool. *7*, 1914: 167 (name, N. Atlantic).

Chauliodus schmidti Ege, 1948

Study material. Thirty-five specimens, 49 to 199 mm standard length from the eastern Atlantic.

Distinctive characters. Chauliodus schmidti is distinguished by the forward position of its dorsal fin, the low number of serial photophores, and the presence of only two larger pigmented light organs in each section of the SM series.

Description. Proportional measurements of the study material expressed as mean percentages of standard length unless noted otherwise, with the range of variation in parentheses.

Body: depth 8.4 (6.3-10.7).
Head: 13.8 (12.2-14.9).
Eye: 3.1 (2.4-4.1); 22.4% of head (18.4%-27.8% of head).
Snout: 3.3 (2.8-3.7); 23.9% of head (20.4%-26.6% of head).
Distance from snout: to origin of dorsal fin 21.4 (19.4-23.4); to origin of anal fin 84.5 (82.8-85.8); to origin of ventral fin 42.9 (39.9-46.0).
Pre-anal length without head: 71 (68-72).
Dorsal fin: rays 6, rarely 5.
Anal fin: rays 10-12.
Pectoral fin: rays 11-13.
Ventral fin: rays 7.
Vertebrae: 52-55 [56].
Branchiostegal rays: 17-19.
Serial photophores: Ventral row: IP 9-11; PV 17-20; VAV 22-25; AC 9-11; Total 60-63. Lateral row: OV 17-20; VAL 21-24; Total 38-42.

Body elongate, slender, compressed, the depth averaging about 1/12 of the standard length. Chin barbel reduced to a stump, at least in adults.

Head 1/8 to 1/7 of standard length, bony ridges present above eyes. Eye round, its diameter averaging a little more than 1/5 head length. Snout generally slightly longer than eye.

Subocular organ present below front of eye, deeply embedded. Postocular organ round, below posterior part of eye.

Mouth large, jaws almost equal to head. Premaxillaries with four teeth, second tooth longest, fourth tooth generally longer than third. Maxillaries with numerous oblique denticles on posterior part of ventral margin, entering gape. Mandibles with five to nine (most often six) larger teeth, and none to two small denticles posteriorly near corner of mouth.

Pectoral fins arising low on body, below posterior part of opercular apparatus, of 11 to 13 rays. Origins of ventral fins close together at midventral line, before middle of standard length, fins with 7 rays. Dorsal with six, rarely five rays, dorsal origin over 5th to 7th OV photophore. Anal origin far behind dorsal, close to caudal, fin with 10 to 12 rays. Caudal fin forked.

Sides of body with five longitudinal rows of scales, the scale areas marked by pigment patterns. Each scale area with one to several small photophores, those of the second row generally with one, sometimes two, of the third and fourth rows with two such organs. Serial photophores located ventral to scale areas of fifth row. SM organs with two larger, pigmented organs in each section, SM formula 1+2+1.

Size. The largest known specimen is something over 200 mm long.

Relationships. C. schmidti is very close to *C. sloani* of the Atlantic, differing from that group in the lower number of serial photophores, and in a tendency for the scale areas of the second row to have only a single small light organ more often than two (see Table II). It would seem that *C. schmidti* has probably developed directly from the Atlantic population of *C. sloani.*

Range. C. schmidti apparently occurs only in the eastern Atlantic, off the coast of Africa, between approximately 10°S and 20°N. Its east-west distribution is as yet unknown. The species has been found at depths as shallow as 25 meters and as great as 3000 meters. The Dana records (Ege, 1948) show that of their 96 specimens, approximately 48 per cent were taken at depths of 50 meters or less, and about 40 per cent came from between 500 and 1500 meters. There seems to be a strong tendency for small individuals, 50 mm or less, to occur above the 500 meter depth, while specimens over 75 mm are most frequently found at depths of 500 meters and more.

Synonyms and references:

Chauliodus sloanei schmidti Ege, Dana Rept., No. 31, 1948: 139 (type descr., type locality "Tropical waters off W. coast of N. Africa; north-eastern South Atlantic, to ca. 8°S."; type specimen Dana Coll. No. St. 4005); Haffner, Systematic Zool., *1* (1), 1952: 113-133 (zoogeogr.).

Chauliodus sloani schmidti Marshall, Aspects of Deep Sea Biology, N.Y., 1954: 66 (name).

Probable synonym:

Chauliodus sloanei (partim) Norman, Discovery Rept., *2*, 1930: 308.

CHAULIODUS SLOANI Bloch and Schneider, 1801

Study material. Three hundred and sixty specimens, 25 to 278 mm in standard length, from the Atlantic Ocean, Gulf of Mexico, Mediterranean Sea, eastern, middle and western Pacific Ocean, and the Indian Ocean.

Distinctive characters. Because of the rather wide variation between populations of *C. sloani*, it is difficult to give a succinct summary of its distinctive characters. In general, *C. sloani* may be characterized by a greater number of serial photophores than any species except *C. macouni*, a round postocular organ, and the origin of the dorsal fin over the 5th to 8th OV photophore except in some variants from the Indo-Pacific region. In these, however, if the dorsal origin is over the 9th or 10th OV photophore, the SM organs are 1+3+1 or 1+4+0 in each section, which will separate them from *C. danae* of the Atlantic.

Description. Proportional measurements of the study material given as mean percentages of standard length, except as noted, with the range of variation in parentheses. Data in brackets from other authors.

Body: depth 7.9 (5.6-12.0).

Head: 13.6 (10.5-16.3).

Eye: 3.1 (2.0-4.3); 23.3% of head (19.1%-32.4% of head).

Snout: 3.3 (2.3-4.2); 24.4% of head (17.9%-32.0% of head).

Distance from snout: to origin of dorsal fin 21.4 (17.6-25.8) [27.9]; to origin of anal fin 84.8 (80.8-88.4); to origin of ventral fin 42.1 (38.5-50.0).

Pre-anal length without head: 71 (66-76).

Dorsal fin: rays 6, rarely 5 or 7.

Anal fin: rays 10-13.

Pectoral fin: rays 11-14.
Ventral fin: rays 7, rarely 6 or 8.
Vertebrae: 54-62.
Branchiostegal rays: 15-21.
Serial photophores: Ventral row: IP 8-11; PV 18-22; VAV 24-29; AC 9-13; Total [62] 63-70 [72]. Lateral row: OV 17-22; VAL 23-29; Total 42-49.

Body slender, elongate and compressed, its depth averaging less than 1/12 of the standard length. Chin barbel present in young, slender, tapered, flexible, becoming reduced to a short, triangular stump in adults. Indo-Pacific populations have slightly longer barbels than do Atlantic specimens, and appear to retain the fully developed barbel longer.

Head 1/10 to 1/6 of standard length, bony ridges above eyes. Eye round, its anterior-posterior diameter averaging almost 1/4 of head length, and a little shorter than snout. Snout short, but generally slightly longer than eye. Subocular organ present below anterior part of eye, deeply embedded. Postocular organ round, below posterior part of eye.

Mouth large, jaws almost equal to head. Premaxillaries with four teeth, second longest, fourth tooth usually longer than third. Second tooth, and sometimes third and fourth also, slightly barbed. Maxillary longer than premaxillary, with numerous small, oblique denticles on posterior half of its ventral margin, entering gape. Mandible long and heavy, with five to nine (usually six or seven) large teeth, of which the first is much the longest. Behind these, near corner of mouth, 0 to 10 or more tiny denticles (see Table IV).

Pectoral fins arising below posterior edge of opercular apparatus, low on body, fins of 11 to 14 rays. Origins of ventral fins close together on midventral line, before middle of standard length, fins normally of seven rays, rarely six or eight. Dorsal with six (rarely five or seven) rays, its origin over the 5th to 8th OV photophore in Atlantic and Mediterranean populations, as far posterior as the 10th OV photophore in some Indo-Pacific individuals. Anal origin far behind dorsal, close to caudal, fin of 10 to 13 rays. Caudal fin deeply forked.

Sides of body with five longitudinal rows of scales, each scale area marked off by the underlying pigment pattern in skin. Each scale area with one to several small light organs, those of the second row with one or two organs, those of the third row with two, fourth row with one to three, most often two. In temperate Atlantic forms, the two organs of the second row are usually unpigmented. In most of the Pacific, Indian and tropical Atlantic populations, the more ventral of the two organs in the second row is usually pigmented. In some Pacific populations, the small unpigmented organ is reduced or absent, and the same is true of many specimens from the Mediterranean Sea. Large serial photophores located ventral to scale areas of fifth row. SM organs vary in number from one population to another. In most Atlantic forms, usually 1+2+1, in Indo-Pacific forms basically 1+3+1 or 1+4+0, with many variations in the number of small anterior and posterior organs.

Size. The largest specimen examined was 278 mm (11 inches) in standard length. Zahl (1953:603) records one from the Mediterranean of 350 mm, which appears to be the largest known.

Relationships. Chauliodus sloani is the most basic form among the modern species of the genus. At least two species, *C. pammelas* in the Indian Ocean, and *C. schmidti* in the Atlantic, appear to have been derived directly from it. *C. macouni* of the North Pacific and *C. danae* from the Atlantic, although undoubtedly derived from a *sloani*-like form, nevertheless show rather more basic differences which suggest that their origins are more remote than those of *C. pammelas* and *C. schmidti.* And *C. barbatus* is obviously the farthest removed, morphologically speaking, from the basic type.

Range. Of world-wide distribution in tropical and temperate seas. In the Indo-Pacific, it is found as far south as approximately 42°S, and north to roughly 32°N. In the Atlantic, the species has been recorded between 36°S and 57°N, with a single record of a specimen washed up on the southeast coast of Iceland at approximately 65°N. It has also been recorded from many stations in the Mediterranean Sea.

Discussion. The description and characterization of *C. sloani* is not made easier by the distressing tendency of this form to split into races which show greater or lesser morphological differentiation, one from another. This has been thoroughly demonstrated by Ege (1948), and is well shown in his illustrations of the condition of the small body photophores in various samples. Although the differences are not as constant as Ege apparently believed, nevertheless, they do represent tendencies within each population. There is, for example, a trend towards pigmentation of both the small light organs in the second scale row in the tropical forms, while in the populations from temperate areas, these organs tend to be unpigmented. Yet at the same time, greater or lesser numbers of individuals will be found in any of these populations which do not agree with the majority.

Perhaps even more striking is the change in the SM organs with geography. The basic formula in the Indo-Pacific area appears to be 1+3+0, that is, one unpigmented organ at the anterior end of each section, followed by three pigmented organs. But as one progresses eastwards through the Pacific, especially in the Pacific Equatorial Water mass, this formula tends towards 1+3+1 and finally 1+4+0. As far as this particular feature is concerned, it suggests that *C. barbatus,* inhabiting the eastern extreme of the Pacific Equatorial Water, is the end result of whatever forces are at work here, for this species normally has five to seven small pigmented organs in each SM series.

Movement away from the tropics, in a north-south direction, is also reflected in changes in the SM organs. In northern areas of the Pacific, between about 20°N and 32°N, the few specimens available to us showed suggestions of reduction of the pigmentation of the last SM organ. In the temperate Atlantic, both north and south, this condition is much more marked, with perhaps the majority of specimens exhibiting a 1+2+1 condition.

A third characteristic is the length of the barbel, which is shortest in the North Atlantic forms and longest in those from the mid-Pacific. The Indian Ocean specimens are intermediate. Also, the Atlantic *C. sloani* appear to lose their barbels at a smaller size than do the Indian and Pacific ocean members of the species.

All in all, these phenomena are open to at least two interpretations. The first is that each population is more or less isolated by the physico-chemical conditions of the water mass in which it lives, and that the small differences observed from one population to another are the result of reduced genetic interchange between populations as compared to within populations. Without a doubt, this factor is operating but to what extent we cannot tell.

It is also possible to interpret these slight changes in morphology as representing the result of the direct response of the organisms to physical and chemical characteristics of the particular water mass in which they live. We rather lean towards this interpretation, for we find that *C. sloani, sensu stricto,* occurs in nearly all the water masses of the Indian, Pacific and Atlantic oceans. Water mass boundaries do not appear, on the basis of present information, to be serious barriers for this species.

As far as considering these populations as subspecies is concerned, we have already shown that none of them meet the modern criteria for such a division. There is greater difference, for example, between the North Atlantic and Indian Ocean populations of *C. sloani* than there is between the "*secundus*" and "*dannevigi*" groups, yet no one has yet suggested — nor do we do so now — that the two former groups should be designated as other than populations.

Synonyms and references:

Chauliodus sloani Bloch and Schneider, Systema Ichthylogiae, Berlin, 1801: 430 (type descr.); Cuvier, Regne Animal, Paris, 1836-1849: 232 (descr.); Cuvier and Valenciennes, Histoire Naturelle des Poissons, Paris, Vol. *22,* 1849: 382-389 (descr., synonymy); Canestrini, Fauna d'Italia. Pesci., Milan, 1871-1872: 221 (not seen); Döderlein, Atti Accad. Palermo, (2) *6,* 1878-1879: 56 (name); Jordan and Gilbert, Bull. U.S. Nat. Mus., *16,* 1882: 285 (descr.); Facciola, Nat. sicil., *2,* 1883: 188 (not seen); Jordan, Rep. U.S. Comm. Fish., (1885) 1887: 834 (name); Agassiz, Bull. Mus. Comp. Zool. Harvard, *15,* 1888: fig. 214 (illus.); Vaillant, Exped. Sci. Travailleur et Talisman, 1888: 102 (Morocco); Carus, Prodromus Faun. Med., Stuttgart, vol. *2,* 1889-1893: 570 (name); Goode and Bean, Oceanic Ichthyology, Washington, 1895: 96-97, fig. 115 (descr., illus.); Garman, Mem. Mus. Comp. Zool. Harvard, *24,* 1899: 272-274, Pl. K, fig. 3 (name, comp. with other spp.); Odon de Buen, Bol. Soc. esp. Hist. nat., *2,* 1902: 104-105 (descr.); Jordan and Starks, Bull. U.S. Fish. Comm., *22* (1902) 1904: 579 (name); Regan, Trans. Linn. Soc. Lond., (2) *22,* Zool., 1908: 218 (N. of Peros Banhos Atoll); Weber, Siboga Exped. Fische, 1913: 12-13 (descr.); Weber and de Beaufort, Fishes Indo-Australian Archipelago, Leiden, vol. *2,* 1913: 110, fig. 38 (descr., illus.); Sanzo, Mem. R. Accad. talassogr. ital., *39,* 1914: 1-7, figs. 1, 2 (descr. larvae); Gilbert, Proc. U.S. Nat. Mus., *48,* 1915: 321 (name); Sanzo, R.C. Accad. Lincei, (5a) *27,* 1918: 91-97 (descr. larvae); Gilchrist, Rep. Fish. Mar. Biol. Surv. South Africa, No. 2, Spec. Rep. No. 3, 1921 (1922): 42, 54 (occurrence S. Afr.); Jordan, Evermann and Clark, Rep. U.S. Comm. Fish., (1928) 1930, App. X: 71 (name); Borodin, Bull. Mus. Comp. Zool. Harvard, *72* (3), 1931: 64 (name, stomach contents); Fowler, Bull. Amer. Mus. Nat. Hist., *70*, 1936: 219-221, 1199 (name, descr.); Bigelow and Schroeder, Fish. Bull., U.S., *74* (vol. 53), 1953: 145-146 (descr.); Tchernavin, Summary of the feeding mechanisms of a deep-sea fish, *Chauliodus sloani*. Brit. Mus. (Nat. Hist.), London, 1953: 101 pp. (anat. head region in relation to feeding); Munro, Marine and Freshwater Fishes of Ceylon, Canberra, 1955: 35 (Gulf of Manar, 500 fath.).

Chauliodus setinotus Bloch and Schneider, Systema Ichthyologiae, Berlin, 1801: 555, pl. 85 (type descr., illus., type locality Mediterranean Sea); Bonaparte, Iconografia Fauna Italica, III. Pesci., Roma, 1832-1841: fasc. XXX, No. 158, fig. 2 of un-numbered plate (descr., illus.); Catologo Metodico, Napoli, 1846: 35 (name).

Esox stomias Shaw, General Zool., vol. 5 (1), London, 1804: 120, pl. 111 (descr.).

Stomias boa (*Chauliodus schneideri*) Cuvier, Regne Animal Illus., Poissons, Paris, 1817: pl. 97, fig. 3 (illus., not seen).

Stomias schneideri Cuvier, Regne Animal, Paris, 1836-1849: pl. 97, fig. 3 (illus., plate erroneously labelled *Stomias boa*).

Chauliodus schneideri Risso, Histoire Naturelle des Principales Productions de l'Europe Meridionale, vol. III, Paris, 1826: 442, pl. 14, fig. 37 (not seen).

Leptodes sloanii Swainson, Nat. Hist. Classification Fishes, Amphibia, Reptiles, London, 1839: 298 (name).

Chauliodus sloanii (Günther, Cat. Fish. Brit. Mus., vol. 5, London, 1864: 392 (descr.); Goode, Proc. U.S. Nat. Mus., *3*, 1880: 483 (off So. New England); Vinciguerra, Ann. Mus. Stor. nat. Genova, *22*, 1885: 469-470 (descr.); Günther, Handbuch Ichthyol., Wien, 1886: 453, fig. 324 (not seen); Challenger Rept., Zool. *22*, 1887: 179 (New Guinea, Japan, Atlantic, Bermuda, 565-2575 fath. water); Alcock, Ann. Mag. Nat. Hist., (6) *4*, 1889: 399 (Bay of Bengal, Gulf of Manar); Collett, Bull. Soc. Zool. France, *15*, 1890: 223 (Funchal); Alcock, Ann. Mag. Nat. Hist., (6) *8*, 1891: 127 (occurrence Indian O., ova, pyloric caeca); Descriptive Cat. Indian Deep Sea Fishes, Calcutta, 1899: 355 (not seen); LoBianco, Mitt. Zool. Sta. Neapel, *15*, 1902: 419, 420, 422, 431 (juveniles, Gulf of Naples); Regan, Ann. Mag. Nat. Hist. (9) *11*, 1923: 614 (no. vert.).

Chauliodus sloanei Goode and Bean, Bull. Essex Inst., *11*, 1879:

22 (in stomach of cod, Georges Bank); Jordan and Evermann, Bull. U.S. Nat. Mus., *47* (1), 1896: 585 (descr.); Richard, Bull. Mus. Oceanogr. Monaco, *41*, 1905: 12 (name, N. Atl., 0-3000 m); Brauer, Ergebn. Deutsche Tiefsee-Exped. "Valdivia," *15*, Syst. Teil, 1906: 40-42, figs. 7-9 (descr., illus.); *ibid.*, Anat. Teil, 1908: 48-59 (structure photophores), 176, (eyes); Zugmayer, Res. Camp. Sci. Monaco, *35*, 1911: 63-65 (descr.); Murray and Hjort, Depths of the Ocean, Macmillan, London, 1912: 603, fig. 454 (illus., name); 611 (name); Pappenheim, Deutsche Südpolar Exped., *15*, Zool. *7*, 1914: 167 (N. Atlantic); Bierbaum, Z. wiss. Zool., *111*, 1914: 300-301 (structure ear); Roule, Res. Camp. Sci. Monaco, *52*, 1919: 26 (name, Med., Azores); Saemundsson, Vidensk. Medd. naturh. Foren. kbh., *74*, 1922: 177 (SE coast Iceland); Barnard, Ann. S. Afr. Mus., *21*, 1925: 141 (off E. London and Durban); Regan and Trewavas, Dana Rept., No. 5, 1929: 32-34 (descr., range), fig. 24 (illus.); Beebe, Zoologica, N.Y. *12* (1), 1929: 10-12 (descr. young); Norman, Discovery Rept., *2*, 1930: 308 (S. Atl., partim); Roule and Angel, Res. Camp. Sci. Monaco, *79*, 1930: 24, pl. 1, fig. 23 (larvae, Canaries, Azores, Med.); Res. Camp. Sci. Monaco, *86*, 1933: 81 (name); Beebe, Zoologica, N. Y., *22* (14), 1937: 201 (300-1000 fath., Bermuda); Parr, Bull. Bingham Oceanogr. Coll., *3* (7), 1937: 58 (Bahamas, Bermuda); Bertin, Bull. Mus. Hist. Nat. Paris (2) *11*, 1939: 382 (name); Norman, Sci. Rept. John Murray Exped., *7* (1), 1939: 21 (name, Zanzibar, Maldives); Nybelin, Göteborg. Vetensk. Samh. Handl., (B) *5* (16), 1948: 30 (NE Atl.); Ege, Dana Rept., No. 31, 1948: 1-148 (classification, phylogeny, zoogeogr.); Tchernavin, Proc. Zool. Soc. London, *118*, 1949: 129-143 (cranial anat., mechanics swallowing); Haffner, Systematic Zool., *1* (3), 1952: 112-133 (zoogeogr.); Grey, Fieldiana: Zool., *37*, 1955: 277 (Bermuda, stomach contents).

Chauliodus dentatus Garman, Mem. Mus. Comp. Zool. Harvard, *24*, 1899: 273-274 (type descr., type locality Society Is., type specimen Harvard Mus. Comp. Zool., No. 6597); Beebe, Zoologica, N.Y., *12* (1), 1929: 12 (name).

Chauliodus dannevigi McCulloch, Biol. Res. "Endeavour," *4* (4), 1916: 179-181, pl. LII (type descr., illus., type locality 30 mi. S. of Cape Everard, Victoria, Australia, 180-240 fath.); Regan and Trewavas, Dana Rept., No. 5, 1929: 32 (name).

Chauliodus atlantis (partim) Barbour, Proc. New Engl. Zool. Club, *19,* 1942: 46, pl. XX (type descr., illus., type locality 21°46'N, 83°25'W, type specimen Harvard Mus. Comp. Zool., No. 35621).

Chauliodus danae Phillipps, Rec. Dominion Mus., *1* (1), 1942: 53-54 (misidentification).

Chauliodus sloanei sloanei Ege, Dana Rept., No. 31, 1948: 1-148 (classification, phylogeny, zoogeogr.); Haffner, Systematic Zool., *1* (3), 1952: 112-133 (zoogeogr.); Koefoed, Rep. Sars N. Atlantic Deep Sea Exped., *4* (2) (5), 1956: 18-19 (N. Atl., misc. discussion).

Chauliodus sloanei dannevigi Ege, Dana Rept., No. 31, 1948: 1-148 (classification, phylogeny, zoogeogr.); Haffner, Systematic Zool., *1* (3), 1952: 112-133 (zoogeogr.).

Chauliodus sloanei secundus Ege, Dana Rept., No. 31, 1948: 1-148 (classification, phylogeny, zoogeogr.), 139 (type descr., type locality N. of Samoa Is., 300 m, type specimen Dana Coll., No. St. 3588 (2)); Haffner, Systematic Zool., *1* (3), 1952: 112-133 (zoogeogr.).

REMARKS ON THE SYNONYMY

Chauliodus barbatus

The most easily distinguished species of the genus, it does not appear to have been given any other name, nor have we found any indication in the literature that it has been reported under a mis-identification. Indeed, it is so different from the other species of the genus that mis-identification hardly seems possible.

Chauliodus danae

Known only from the Atlantic Ocean, this is a well-defined species, with a rather lower number of serial photophores than *C. sloani.* Although Pappenheim (1914: 167) gave no characteristics for his 22 mm specimen of "*C. pammelas*" from the North Atlantic (24°41'N, 32°21'W), it seems probable that the specimen had rather fewer photophores than *C. sloani*, leading him to name it as he did. This, together with the locality of capture, strongly suggests that the specimen was actually *C. danae.*

As Ege (1948: 101) has shown, "*C. danae*" of Phillipps, from Cook Strait, must belong to the "*dannevigi*" population of *C. sloani.*

We have examined the types and paratypes of Barbour's (1942:46) *C. atlantis,* and find that the specimens "too small to be determined with any certainty" belong to *C. danae.*

Chauliodus macouni

We have examined the type specimen of *C. emmelas* in the U.S. National Museum, comparing it directly with the type and other material of *C. macouni* in the same institution. There can be no doubt that the two species are identical. The confusion that has arisen over Jordan and Starks' (1904: 579) statement that the head of *C. emmelas* is 7.5 in length, as compared with "about one sixth" in *C. macouni,* is due entirely to the fact that Jordan and Starks used total length, whereas Bean (1891: 44), in describing *C. macouni,* used standard length. As we have shown, there is no justification for retaining *C. macouni* as a subspecies of *C. sloani.*

Chauliodus pammelas

Ege (1948: 101) points out that some specimens of "*C. sloani*" described by Alcock (1899: 144) have only 61 photophores in the ventral row, which is below the number known for *C. sloani.* It is apparent, then, that these specimens must belong to *C. pammelas.* Pappenheim's specimen of "*C. pammelas*" from the Atlantic has already been discussed under *C. danae.* As with *C. macouni,* we find sufficient divergence between *C. pammelas* and *C. sloani* to indicate that the former cannot be considered as a subspecies of the latter. We have therefore placed *C. s. pammelas* as a full species.

Chauliodus schmidti

Ege (1948: 101) has pointed out that at least some of the material reported as *C. sloani* by Norman (1930: 308) probably belongs to *C. schmidti,* for "the two northernmost catching places, . . . fall within an area off the west coast of Africa, where *Ch. sloanei sloanei* is replaced by the new subspecies *Ch. sloanei schmidti.*"

We have shown above that this form must be regarded as a species closely related to, but separate from *C. sloani.*

Chauliodus sloani

The various ancient names applied to this species are listed in the synonymy, and would seem to present no problems worth noting. A number of authors have followed Swainson (1839) and Günther (1864) in spelling *sloani* with two i's. There is no justification for this, except that it was possibly the fashion in the first half of the 19th century to use this form. Goode and Bean (1879) used the spelling "*sloanei,*" and Jordan and Evermann (1896), evidently justifying their change to this emendation, noted that the species was named for Sir Hans Sloane. However, the spelling of patronymics in those days was a casual matter, and Sir Hans himself was doubtless not entirely certain of the correct spelling. We prefer to maintain Bloch and Schneider's (1801) original orthography of "*sloani.*"

We have examined the type specimen of Garman's *C. dentatus* (Harvard Mus. Comp. Zool., No. 6597), a species long considered distinct because of Garman's (1899) indication that there were 14 AC photophores. Although the specimen is broken in three pieces, nevertheless it is possible to fit the parts together with a fair degree of precision. We counted 10 AC organs, with probably one, possibly two missing from the break in the caudal peduncle, for a maximum AC count of not more than 12. The total count of the ventral row of photophores is either 69 or 70, of the lateral row 48. These counts fall within the upper limits observed for *C. sloani,* and since all other characteristics of the specimen agree well with that species, we have placed *C. dentatus* Garman in the synonymy of *C. sloani.*

Examination of the type and paratype (Harvard Mus. Comp. Zool., Nos. 35621 and 35615) of *C. atlantis* Barbour shows that this species belongs in *C. sloani.* The smaller specimens accompanying the types have already been remarked on.

Chauliodus dannevigi McCulloch falls well within the normal variation of *C. sloani,* according to McCulloch's (1916: 179) description, and is therefore included as a synonym. As Ege (1948) showed, this form represents a more or less discrete group, which Ege considered a subspecies. We find ourselves unable to agree with this interpretation, considering *dannevigi* to represent a population no more divergent than several others, e.g. that from the Sulu Sea. The same is true of the form described by Ege as *C. sloanei secundus,* as shown in the early pages of the present paper.

SUMMARY

Specimens of all known species of *Chauliodus* have been examined, including the types of *C. barbatus, C. macouni, C. emmelas, C. dentatus,* and *C. atlantis.* As a result, only six species of *Chauliodus, C. barbatus, C. danae, C. macouni, C. pammelas, C. schmidti* and *C. sloani*, are maintained. All other species have been found to be synonyms. The several subspecies proposed by Ege have been shown to be either fully recognizable as species or else to be no more distinct than more or less discrete populations of *C. sloani.*

LIST OF SPECIMENS[1]

Chauliodus barbatus. Harvard Mus. Comp. Zool., Nos. 28489, 28490 (types); U.S. Nat. Mus., Nos. 148239, 151225; Zool. Mus. Univ. Copenhagen, "Galathea" Coll., Nos. 12, 13, 14, 15; Stanford Univ. Zool. Mus., No. 25314; Scripps Inst. Oceanogr., Nos. 52-363 (2), 52-390, 52-404, 55-244, 55-246, 55-258 (3), 55-265.

Chauliodus danae. Bingham Oceanogr. Coll., Nos. 2928 (6), 2929 (3), 2931, 2932, 2933, 2934 (2), 2935, 2936 (2), 2937, 2938 (5), 2939 (6), 2940 (4), 2941 (2), 3211 (3), 3766, uncatalogued (8); Harvard Mus. Comp. Zool., Nos. 32277 (2), 34956 (9), 34983 (2), 35165, 35620 (3); U.S. Nat. Mus., Nos. 89914, 100336, 100565, 117872, 117874 (2).

Chauliodus macouni. U.S. Nat. Mus., Nos. 45372 (type), 51464 (type of *C. emmelas*), 53946, 77462, 125340, 132131 (2), 150088, 150089, 150090; U.S. Fish Wildl. Serv. Lab., Honolulu, Nos. 1778 (3), 1780 (3), 1781, 1783; Stanford Univ. Zool. Mus., Nos. 2000, 5259, 24950 (7); Scripps Inst. Oceanogr., Nos. 51-373 (4), 53-332 (3); Univ. Wash. Coll. Fish., uncatalogued (2); Univ. Wash. Dept. Oceanogr., uncatalogued (57).

Chauliodus pammelas. British Museum (Natural History), Nos. 1939.5.24.410, 1939.5.24.411, 1939.5.24.413, 1939.5.24.414, 1939.5.24.415, 1939.5.24.416, 1939.5.24.417.

Chauliodus schmidti. Marinbiol. Lab. Charlottenlund, Dana Coll., Nos. 3999 I, 4000 VI, 4000 X, 4003 V, 4003 VII (2), 4004 I (3), 4005 I, 4005 III, 4005 V, 4005 VII (7), 4006 I (8), 4006 II, 4007 I (3), 4007 VI (3), 4007 IX.

Chauliodus sloani. Bingham Oceanogr. Coll., Nos. 415 (2), 2915, 2916 (2), 2917 (2), 2918 (5), 2919, 2922 (4), 2924, 2925,

[1] Numbers in parentheses indicate number of specimens if more than one.

uncatalogued (4); Harvard Mus. Comp. Zool., Nos. 3903 (13), 26405 (2), 31607 (4), 31608 (6), 31609, 31610, 32274, 32275, 32276, 34949, 34952 (5), 34954 (2), 34978, 34982 (2), 35095, 35099, 36598, 39433 (5), 39726; Marinbiol. Lab., Charlottenlund, Dana Coll., Nos. 3676 II (3), 3678 IV (4), 3678 VI, 3680 VI (7), 3680 VIII (4), 3681 I (4), 3682 I, 3683 I (3), 3683 IV (6), 3683 VI (5), 3683 VII, 3684 VI (2), 3685 I (21), 3685 IX (3), 3686 VIII (4), 3735 I (6), 3735 II (6), 3736 I (8), 3736 III (5), 3736 V (9), 3736 VI (2), 3737 I (18), 3737 II, 3738 I (8), 3738 II, 3738 III (2), 3739 I (4), 3739 VI, 3739 VII, 3739 IX (2), 3740 I (4), 3740 II (2), 3925 II (3), 3933 III. 3949 I (2), 3953 I (2); as *C. sloanei dannevigi* 3587 IX, 3601 I (2), 3613 VI, 3624 I, 3625 I, 3627 VI, 3630 II, 3631 II (2), 3631 III, 3639 I, 3640 I, 3640 III, 3651 I (3), 3651 VI, 3653 I, 3654 I, 3655 V (4), 3656 I, 3656 III, 3663 I, 3663 VIII (3), 3664 IV (3); as *C. sloanei secundus* 3584 I, 3716 II (2), 3766 VIII (5), 3766 XIII, 3768 V, 3809 II (23), 3830 V (2), 3881 I (4), 3881 II (5), 3934 I+VI+XI (3), 3934 II+VII+XII (5), 3934 III+VIII+XIII (4), 3951 I, 3969 IV; Scripps Inst. Oceanogr., No. 52-404 (3); U.S. Fish Wildl. Serv. Lab., Honolulu, 1782, 1917, 1918, 1919 (2), 1922, 1923, 1924 (2), 1926 (2), 2336, 2338, 2339 (2), 2340, 2341; U.S. Nat. Mus., Nos. 39218, 44402, 89915, 92246 (2), 117873, 131598, 143060, 158832, 159889, 163490 (2), 185590, 185591 (6), 185592 (2), 185593, 185594; Univ. Miami Mar. Lab., Nos. 590, 716, 1623, 1632, 2004.

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